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Final Report

To the Office of Naval Research

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1. Introduction

Observation and sampling of a species over a wide area will show its distribution and abundance; inferences can then be drawn as to the causes of these limits by correlations with environmental variables, both physical and biological. As in all other branches of sciences, however, only experiments can test the validity of these inferences, and experiments require, not a wide survey, but intensive observations in one place over a period of time. The place is usually the laboratory; with care, however, experiments can also be done under natural conditions. I feel that in ecological studies, where the complexity of interactions is very great, experiments under natural conditions are necessary to supplement laboratory experiments. Both are necessary at this stage of development of ecology. Complete understanding will come only when all aspects have been dealt with in the laboratory.

Such outdoor experiments are difficult to do in the subtidal benthos or pelagic realms. In the intertidal region they are feasible; I believe that the results of intertidal experiments can be used as models to explain the ecology of subtidal benthic species which are beyond the reach of most experimental methods.

2. Methods

This study was made during three complete summers (June through August) of 1959, 1960 and 1961, and in three shorter visits in December 1959, March 1961 and June 1962, for a total of 36-1/2 weeks. The study areas were visited almost every day, 240 visits in all.

The study was restricted to two areas on San Juan Island, north of Puget Sound, Washington. The first was on the grounds of the Friday Harbor laboratories of the University of Washington, located on a large concrete pier piling under the "Cantilever pier." The second was on the opposite (western) side of the island, just south of Pile Point, and about 500 yards north of Kanaka Bay. The eastern area (Cantilever pier) is characterized by swift tidal currents but only slight wave action; the western area (Pile Point) has, at times, strong wave action as well as swift tidal currents; being in Puget Sound, it does not experience the severe wave action of the outer Pacific coast.

A few other areas on San Juan Island were visited; one in particular, Westcott Bay, is characterized by very quiet water with muddy shores with rocks imbedded in the mud.

In each of the two main areas, barnacles were studied by counts and photographs of marked areas. Some areas were protected from predators by stainless steel wire mesh cages, similar to those described in Connell (1961a). Rocks or mussel shells bearing barnacles were transplanted from one level to another. Predatory animals, particularly three species of *Thais* (gastropods), were counted on these areas, individually marked and observed for growth and movements. Some were enclosed in cages with barnacles to measure rates of feeding on the barnacles. Similar measurements of feeding rates of both the three species of *Thais* and the nudibranch *Onchidoris fusca* were made in an outdoor aquarium at the laboratory. This aquarium had a simple siphon arrangement to produce a continual "tidal" change in water level so that the animals had periods of exposure to air.

The species studied in detail were:

Barnacles: Balanus glandula
Balanus cariosus

Predators: Thais emarginata
Thais canaliculata
Thais lamellosa
Pisaster ochraceous (starfish)
Onchidoris fusca

Other species observed in lesser detail were:

Chthamalus dalli (barnacle)
Purpura foliatum (snail)
Fusitriton oregonensis (snail)
Searlesia dira (snail)
Amphissa versicolor (snail)
Leptasterias aequalis (starfish)
Fish: various shore species, mainly blennies

The following account of the results will not include the full details which have been reported in the earlier annual progress reports, but will be, as directed by the ONR regulations: "A summary of all work accomplished, including details on results not previously reported." Since only one week's visit (June 1962) was made since the last report, this final report will be mainly a summary of the whole research project.

3. Barnacles

The two species of Balanus show a peculiar "complementary" difference in the distribution of adults between shore levels. B. glandula exists as an adult only at the extreme upper fringe of the intertidal zone, so that the size is large at the top, decreasing abruptly to smaller (young of the year) at lower levels. B. cariosus adults begin below the zone of adult glandula and gradually increase in size as one proceeds down the shore. The lower limit of adult B. cariosus is also abrupt at about mean low water, although young of the year are found settled down to extreme low water level. All the observations and experiments were designed to elucidate the canals of these peculiar distributions.

a. Balanus glandula

The distribution of B. glandula described above was found at all areas visited except in two situations, which, with the results of certain experiments, serve to reveal the causes of its distribution:

(1) In Westcott Bay, adults occur down to mean low water level.

(2) On vertical smooth surfaces, such as the concrete piling at Cantilever pier, or on a huge natural limestone boulder on the west shore, there are no adults at any level, although many young attached each year.

(3) In the tidal aquarium, all three species of Thais chose B. glandula in preference to B. cariosus when offered equal numbers of similar-sized individuals of each species of barnacle.

(4) In Westcott Bay, only a few Thais occur, in contrast to the usual dense populations on other areas.

(5) On the Cantilever pier piling, Thais were observed to climb up at high tide to the upper limits of the water level. They were never seen to do so on the rough sloping rocks on the shore 15 feet away. When three cages (excluding Thais) were attached on the piling at the level of the adults on the adjacent shore, the barnacles survived well there. After three years the area inside these cages resembled the adult zone on the shore, with adults of three year-groups and young of the year. Outside the cages none survived a year.

From all these observations it is concluded that the dense populations of Thais on the shore selectively remove the B. glandula from all but the highest levels. On smooth vertical surfaces, Thais has time to ascend at high tide and feed, before the tide drops, so that all B. glandula are removed. In certain quiet areas, such at Westcott Bay, Thais evidently cannot maintain large populations and there B. glandula survives at all intertidal shore levels.

One other interesting confirmatory detail was discovered since the last report. Nine feet away from the Cantilever Pier piling is a wooden tide gauge tube, which is suspended from the pier above, so that it does not touch the bottom. Thus Thais, with no pelagic larvae, cannot get onto this tube, whereas Balanus can. The lower limit of adult B. glandula is at mean low water on the tube, in the absence of Thais, while on the shore about 24 feet away the lower limit is at mean high water level, six feet above that on the tube. Here there is no difference in wave exposure sediment, etc., as there is between Westcott Bay and Pile Point; this result provides a "crucial experiment" confirming the control of B. glandula distribution by Thais predation.

This situation is parallel to that of B. balanoides and Thais lapillus in Scotland and Woods Hole, Massachusetts (Connell, 1961a).

b. Balanus cariosus

The distribution of this species is as different from that of B. glandula as chalk from cheese. Adults and young of B. cariosus both live in zones occupied by three species of Thais, and the size of the adult individuals becomes progressively greater at lower levels. At three levels, the median sizes (scutum length) were 8, 12 and 17, while the smallest individuals were 4, 8 and 12, respectively. Then at about mean low water the adults disappear at a very sharp lower boundary.

The following observations suggest that predation is the cause of both the abrupt lower limit and the progressive change in size. On sunny days the Thais retreat to shaded or damp crevices during low tide. At the following high tide they move out to feed; this was confirmed by observations at successive tides. Since the weather was clear and sunny on most days during the three complete summers which I spent there, it is probably the regular pattern of activity

of Thais during the summer. Individual records showed that all three species of Thais grew mainly during July and August, with slower growth in September and October, and almost no growth during the rest of the year. The mortality rate of the barnacles was highest during the months of growth of Thais. Very few Thais were seen feeding in December and March. Thus it is safe to conclude that the feeding of Thais takes place mainly during the seasons when clear warm days are common. At night and in the cool early morning Thais were scattered over the open rock. In summary during the season of maximum feeding, Thais is usually interrupted in its feeding once a day, during the daylight low water. The length of its uninterrupted period of feeding might be 22 hours near low water level, and only about 13 hours near high water level.

If a Thais were interrupted by a daylight low water before it had managed to open a barnacle, it seems unlikely that it could return from its shelter to the same barnacle and continue its work. Also, larger barnacles take longer to open than smaller ones. The shell of larger barnacles is much thicker, and the opening procedure requires that enough shell be removed so that some tissue is exposed to the action of a (hypothetical) toxin.

Therefore, if a barnacle is so large that the time required to open it is longer than the uninterrupted feeding period, it will be invulnerable. Obviously the "invulnerable size" of barnacles would be larger at lower shore levels, since the period of uninterrupted feeding by Thais is longer there. Below mean low water level, continuous feeding for several days is possible, so that at this level an abrupt change from short interruptions to no interruptions occurs. No barnacle would be invulnerable below this level.

This hypothesis was tested and confirmed by transplanting the largest B. cariosus which I could find down to a level below mean low water. If protected by cages they survived. With Thais enclosed in the cages they were eaten. Exposed without cages they were very quickly eaten. Besides Thais there were Purpura and Pisaster in the area, which, continually submerged in an aquarium, killed and ate very large B. cariosus.

In summary, the abrupt lower limit of B. cariosus is due to the abrupt change to uninterrupted feeding by its predators. In the intertidal region, the fact that the minimum size of adults was 4 at the top, 8 at the middle and 12 at the bottom of the shore can be ascribed to the removal by predators at lower levels of those below the "invulnerable size." The average and maximum sizes are greater at lower levels simply because the growth rates are faster at lower levels.

The question remains of how any individuals ever reach the invulnerable size. The answer is, few do; in the three year period of my observations, no barnacles survived their first year at the lowest level, so that no new adults have entered the population in that time. However the growth and mortality rates are very low among the few very large barnacles at this level. Thus the "turnover" is very slow, and an occasional recruit would be enough to maintain such a population. In such a case chance would play a large rate. Chance fluctuations in weather might affect the recruitment of either the barnacle or Thais.

4. Predators of the barnacles

a. The comparative biology of three species of Thais

The three species will be referred to by the initial letters of their specific designation: E = emarginata, C = canaliculata, L = lamellosa.

(1) Distribution

E is found in the upper half of the shore, usually in crevices. C is lower down, as is L, the ranges overlapping almost completely, although L is usually a bit lower. At higher levels only large individuals of L are found, at lower levels all sizes. On the drier south-facing aspects, all three species are lower on the shore.

(2) Reproduction

E and C lay egg capsules in small groups of from 4 to 23 capsules, whereas L tends to lay its capsules together in large groups; one such group contained about 8500 capsules. The number of fertile eggs laid per female was: E, 150; C, 210; L, 350. Each has about 15 embryos per capsule, but in E's capsule there are about 200-400 non-fertile "nurse" eggs, whereas in the capsules of C and L, all eggs are fertile, and contain large amounts of yolk within each egg.

All lay eggs in the spring and summer; L has been observed laying eggs in other seasons.

(3) Growth and longevity

L takes two to three years to reach maximum size, whereas E and C do so in one and one-half years. Some large marked snails have not grown for three years, so that the length of life after reaching maximum size is not known. In C and L, boring polychaetes in the shells (Polydora) and erosion of the spire by the rasping of small limpets (Acmaea) may eventually limit the length of life.

The growth occurs almost entirely between mid-June and October, when the feeding is most active.

(4) Feeding behavior

[a] Method of opening barnacles

Thais was always seen feeding on a barnacle which had its opercular valves open; the Thais had its proboscis extended between the opened valves. Also, there was always a pit or very small hole drilled either at the juncture of two wall plates, at the base of a plate or at the edge of an opercular valve. These were seldom large enough to admit a proboscis, and no Thais was ever seen feeding through any hole drilled in a barnacle. It is probable that the Thais removes shell until it exposes living tissue, then secretes a toxin which is

eventually carried to the C.N.S. or neuromuscular junctures, causing relaxation of the adductor muscle and opening of the valves. One instance was observed of a Thais lamellosa on the shore in position over a pit (not a hole) drilled in the side of a Balanus cariosus; the opercular valves were relaxed, easily opened by me.

[b] Rates of feeding and digestion

Details are given in previous annual reports, which can be summarized as follows. The number and size of all barnacles eaten both on the shore and in a tidal aquarium were measured, for many individually isolated Thais. L ate fastest, E slowest. Most of the succeeding work was done with L, to which the rest of the section will apply.

Intermediate-sized L ingested more than large or small L, on an absolute basis (6.5 mg./day/Thais). By collecting, drying and weighing the feces, it was found that most L digested about 85% of their ingested food (dry weight). Very small Thais which ate only small barnacles, and larger Thais which were given only small barnacles, digested only 62 and 75%, respectively, of their ingested food.

The lower efficiency of the large Thais which were given only small barnacles was partly due to the fact that they ate the whole barnacle body, exoskeleton included, and then egested the skeleton. Thais eating large barnacles ate only the soft parts, leaving the exoskeleton, and egested less.

As did Thais lapillus in Scotland and Woods Hole, all three species of Thais at Friday Harbor chose large over small barnacles as prey. When offered only small barnacles, L ate up to ten times as many barnacles as when it ate large barnacles. In the former case they ingested only about 60% as much organic matter and were "thinner" (lower ratio of dry body weight to shell weight) after ten weeks than were those which ate large barnacles. This experiment indicates that the behavior leading to the choice of larger barnacles as prey confers a selective advantage; a greater rate of intake of food and greater digestion efficiency should lead to faster growth and higher reproductive rate. There is, presumably, also some selective advantage gained by the choice of B. glandula over B. cariosus as prey by all three species of Thais.

b. Other predators

(1) Onchidoris fusca

This nudibranch feeds intertidally in the winter. Its feeding rate in the aquarium in late August was lower than Thais lamellosa, with also a lower digestive efficiency of only 67%.

(2) Pisaster ochraceous

This large starfish ascends into the intertidal region at high tide, eating many small barnacles and even some large ones. The lower limit of B. cariosus on Cantilever pier is probably due to these starfish, which were often seen feeding on the moderately large B. cariosus at high tide.

(3) Strongylocentrotus drobachiensis

This abundant sea urchin also enters the intertidal zone at high tide, biting off whole small barnacles.

5. Discussion and Conclusions

This study emphasizes the importance of biological interactions in determining the distribution and abundance of organisms. All the recent surveys and reviews of intertidal ecology (see Southward, 195, for a review) draw inferences as to the causes of intertidal zonation patterns from correlations with environmental factors, mainly physical. This is a result of the methods of study, which have involved extensive surveys with no experimental investigations.

Experiments designed to study the effect of physical factors on distribution almost always result in the finding that the limit of toleration of animals and plants are always much greater than those which the animal experiences naturally; thus physical factors are seldom the direct cause of limitation of distribution. From the findings of this and my previous studies (Connell, 1961a, 1961b), it may be suggested that biological interactions play the decisive role in such limitations.

6. References

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